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ARTICLE

Freshwater Ecology

Two decades of watershed research assessing responses of salmonid fish to forest disturbance by harvesting and wildfire

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Abstract

Wildfires are increasingly affecting aquatic systems in forested landscapes in many areas around the world. However, in many forested regions aquatic systems are influenced by a legacy of previous forest disturbance in the form of timber management. As we explore wildfire impacts to aquatic biota in forested streams, it is valuable to contextualize post-fire fish responses relative to past disturbance to understand relative impacts and to acknowledge potential legacy effects. Further, due to the random nature of fire, pre-fire datasets to quantify post-fire effects are rare. Riverscape approaches collected at both high resolution and across broad spatial extents continuously through river systems can offer a powerful approach to capture spatial and temporal variation within watersheds and provide a comprehensive picture of wildfire effects. In our study, we collected a unique spatiotemporal dataset of longitudinal patterns of salmonid fish abundance at a watershed scale over 13 years total before and after multiple forest disturbances in the Hinkle Creek watershed of western Oregon, USA. Focal species and life stages considered in this analysis included resident populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), anadromous populations of steelhead (*Oncorhynchus mykiss*), and young-of-year life stages of both species. We collected data from four distinct time periods, including pre-harvest, post-harvest in the headwaters, post-harvest along the lower mainstem, and after high-severity wildfire with post-fire salvage logging. Longitudinal patterns of salmonid fishes varied between years and with the severity and extent of disturbance. Cutthroat trout and total salmonid abundance (all species and life stages) tended to be greatest in the post-fire periods relative to post-harvest and pre-harvest periods. Longitudinal patterns also revealed that post-fire salmonid fish responses were most likely to occur in the upstream portions of the watershed where temperature increases after wildfire were smaller. Collectively, these data provide a case study illustrating that salmonid fishes can

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be resilient or even enhanced by forest disturbances like wildfire and that responses are likely to vary with the type, severity, and extent of the disturbance. However, responses are likely context-dependent, and more information is needed to further explore the mechanisms responsible for driving post-fire fish responses.

KEYWORDS
cutthroat trout, forest management, forest–stream interactions, logging, rainbow trout, riparian buffer, riparian forest, steelhead trout, stream disturbance, wildfire

INTRODUCTION

Like many regions around the world, wildfire regimes in the Pacific Northwest (PNW) region of North America have been disrupted over the past century and a half due to changing climate, the cessation of Indigenous burning, and a broad policy of fire suppression (Dye et al., 2024; Hagmann et al., 2021; Hessburg et al., 2019; Reilly, Zuspan, et al., 2022). Large-scale forest disturbances still occurred during this period, but they were dominated by forest harvest rather than wildfire (Magerl et al., 2023; Pan et al., 2011; Wissmar et al., 1994). As climate and land use changes have led to increases in frequency of large, high-severity wildfires in the western United States and around the world, it is important to recognize that many of these fires are occurring in landscapes of regenerating forests with a legacy of forest management (Johnstone et al., 2016; Turner et al., 2016). Therefore, assessments of wildfire in these areas are capturing not only the wildfire event, but collective effects of fire on landscapes with a particular disturbance history (Hessburg et al., 2019). Thus, to understand and parse out ecological effects of wildfire disturbances, it may also be important to contextualize responses relative to the impacts of prior forest management activities.

To assess the impacts of forest disturbances on aquatic ecosystems, salmonid fishes are often focal species given that trout, salmon, and charr may be sensitive to changes in stream chemistry, stream temperature, and overall habitat conditions (Baker et al., 1996; Carline et al., 1992; Dunham et al., 2003; Isaak et al., 2010; Poole & Berman, 2001; Wenger et al., 2011). Salmonids often function as the apex predators in headwater stream ecosystems, and as a result, they reflect and integrate processes lower in the food web in these systems and can have important top-down effects on stream food webs and aquatic ecosystem processes (Cooper et al., 2024; Naman et al., 2022; Power, 1990). Therefore, tracking the response of salmonid fishes can be a useful proxy for evaluating the effects of changes in watershed conditions on aquatic ecosystems (Bisson et al., 2009; Fausch et al., 1995; Hicks et al., 1991; Schlosser, 1991).

The PNW region of North America has an extensive history of forest disturbances due to both forest management and wildfires (Bolsinger & Waddell, 1993; Johnston et al., 2023; Magerl et al., 2023; Reilly, Zuspan, et al., 2022). For the wet temperate forests west of the Cascade Mountains of the PNW, the historical fire regime is complex (Johnston et al., 2023). Research has suggested that PNW fire regimes range from relatively infrequent, stand-replacing, mixed-severity fires to relatively small, frequent, non-stand-replacing, low-severity fires (Agee, 1996; Johnston et al., 2023; Keane et al., 2008; Reilly et al., 2017; Walsh et al., 2015). Over the last century, forest management has been the dominant disturbance on these landscapes. Due to active fire suppression, alterations in traditional land use practices, and a degree of random chance, there were generally no large, high-severity wildfires through the middle and late 20th century in the region west of the Cascade Crest (Reilly, Zuspan, et al., 2022). However, in 2020 this region experienced several, large, high-severity wildfires, which burned many actively managed forests (Reilly, Norman, et al., 2022). While this year was anomalous in terms of area burned, model projections indicate that the western United States is likely to continue to experience increases in the frequency of high-severity wildfires due to greater occurrence of droughts, east wind events, ignitions, and lower relative humidity (Dye et al., 2024; Hessburg et al., 2019; Jain et al., 2020; Reilly, Zuspan, et al., 2022).

Across the western United States, responses of salmonid fish to landscape disturbances, such as forest management and wildfire, have been mixed—in large part because the effects of any one disturbance event on fish and other aquatic biota may be linked to the interaction of the disturbance event with additional processes or characteristics of the system (Bixby et al., 2015; Gresswell, 1999; Isaza et al., 2022; Roon, Bellmore, et al., 2025). There are a number of similarities between forest management activities and wildfire in that they remove vegetation from extensive patches of the landscape, altering similar characteristics of watersheds and the streams that they drain, including hydrology, stream temperature, erosion and sedimentation rates, and stream chemistry (Moore & Richardson, 2012; Nitschke,

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2005; Reeves et al., 1995). However, other aspects of these two disturbances may differ in both terrestrial and aquatic systems (McRae et al., 2001; Moore & Richardson, 2012; Nitschke, 2005). For example, while contemporary forest management maintains riparian buffers, wildfire—particularly high-severity wildfire—can kill much of the riparian forest, which can open canopies over streams more than current forest management in this region allows. This has been noted as a potential ecological concern because loss of forest canopies along a stream leads to increased radiation at the stream surface, often resulting in elevated stream temperatures (Koontz et al., 2018; Mccullough et al., 2009; Warren et al., 2022). And, increases in temperature can directly affect the growth and survival of thermally sensitive salmonids that dominate many streams across western North America (Rosenberger et al., 2015; Selong et al., 2001). If the system is a cold headwater stream, the effects on fish may be minor (Roon, Bellmore, et al., 2025; Swartz et al., 2025; Swartz & Warren, 2022; Warren et al., 2022); however, if the system is already near the thermal limits for native fish, increases in temperature associated with loss of canopy cover have the potential to negatively impact coldwater fish (Burton, 2005; Isaak et al., 2010; Koontz et al., 2018; Railsback, 2022).

Based on historical forest management studies that occurred before riparian buffers were a regulatory requirement, logging activities were sometimes linked to declines in fish (Hall & Lantz, 1969). These declines have been attributed, at least in part, to loss of canopy cover, increased stream temperatures, and dramatic reductions in dissolved oxygen (Hall & Lantz, 1969). However, canopy removal was not the only impact of historical forest management on streams. Historical forest management practices often resulted in high sediment loads to the stream channel and a loss of stream structural complexity due to the removal of large wood (Hicks et al., 1991; Megahan & Kidd, 1972). It has been suggested that these changes had a greater long-term negative impact on stream salmonids than canopy removal (Cunningham et al., 2023; Mellina & Hinch, 2009), however, not all early forest management resulted in fish declines. The removal of riparian and upland vegetation during timber harvest has also been linked to increased primary production leading to potential bottom-up increases in salmonid fish in headwater streams (Kaylor & Warren, 2017; Murphy et al., 1981; Wilzbach et al., 2005). Assessing and comparing the effects of contemporary forest management and wildfire to stream biota in the same system may help to parse these drivers and build our understanding of the context around fish responses to large-scale forest disturbances.

In September 2020, the Archie Creek Fire burned over 53,000 ha in the central Cascade Mountains in western Oregon. The fire footprint encompassed the location of a previous long-term study that assessed timber harvest effects on aquatic habitat and fish populations. Thus, we had a unique opportunity to leverage an extensive pre-fire dataset to quantify the effects of wildfire on fish populations across a watershed stream network addressing a common issue in post-fire assessments (Bladon et al., 2008; Dunham et al., 2007). This also provided a rare opportunity for a case study evaluating the effects of fire in the same watershed where we had previously completed a study to quantify the effects of forest harvesting. We leveraged previous long-term data with post-fire fish population assessments to address two core questions. First, how does the mean relative biomass and abundance of trout and steelhead in a headwater stream system after wildfire compare to the relative biomass and abundance of these species before and after forest management in this system? To answer this question, we quantified the relative biomass density (in grams per square meter) and abundance density (in number of fish per square meter) of both coastal cutthroat trout (*Oncorhynchus clarkii clarkii*, hereafter cutthroat trout) and rainbow trout/steelhead (hereafter *O. mykiss*) in pools along 2.5–3.5 km of a small fourth-order stream in the Western Cascade Mountains of Oregon before and after forest management and after wildfire. Our second question asked: How does the longitudinal patterns of relative biomass and density of salmonid fish in pools along the mainstem of a fourth-order stream network compare after wildfire relative to the longitudinal variation before and after forest management?

METHODS

Site description

Hinkle Creek, a tributary of Calapooya Creek, is situated in the Umpqua River Basin in the Western Cascade Mountains of central Oregon (43.423682, −123.040467; Figure 1). Hinkle Creek has two primary sub-basins: North Fork Hinkle Creek (NFHC; 858 ha) and South Fork Hinkle Creek (SFHC; 1083 ha; Figures 1 and 2). The land in both sub-basins of Hinkle Creek is privately owned and managed for timber production. The dominant upland vegetation is Douglas-fir (*Pseudotsuga menziesii*), and riparian vegetation includes regenerating Douglas-fir, red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), salmonberry (*Rubus spectabilis*), Himalayan blackberry (*Rubus armeniacus*), and trailing blackberry (*Rubus ursinus*). The soils are mostly clay loams to silty loams classified as Typic Palehumult or a Typic Haplumbrept (Kibler et al., 2013). The average annual precipitation ranges from 1646 mm at the lower elevations up to 2427 mm at the

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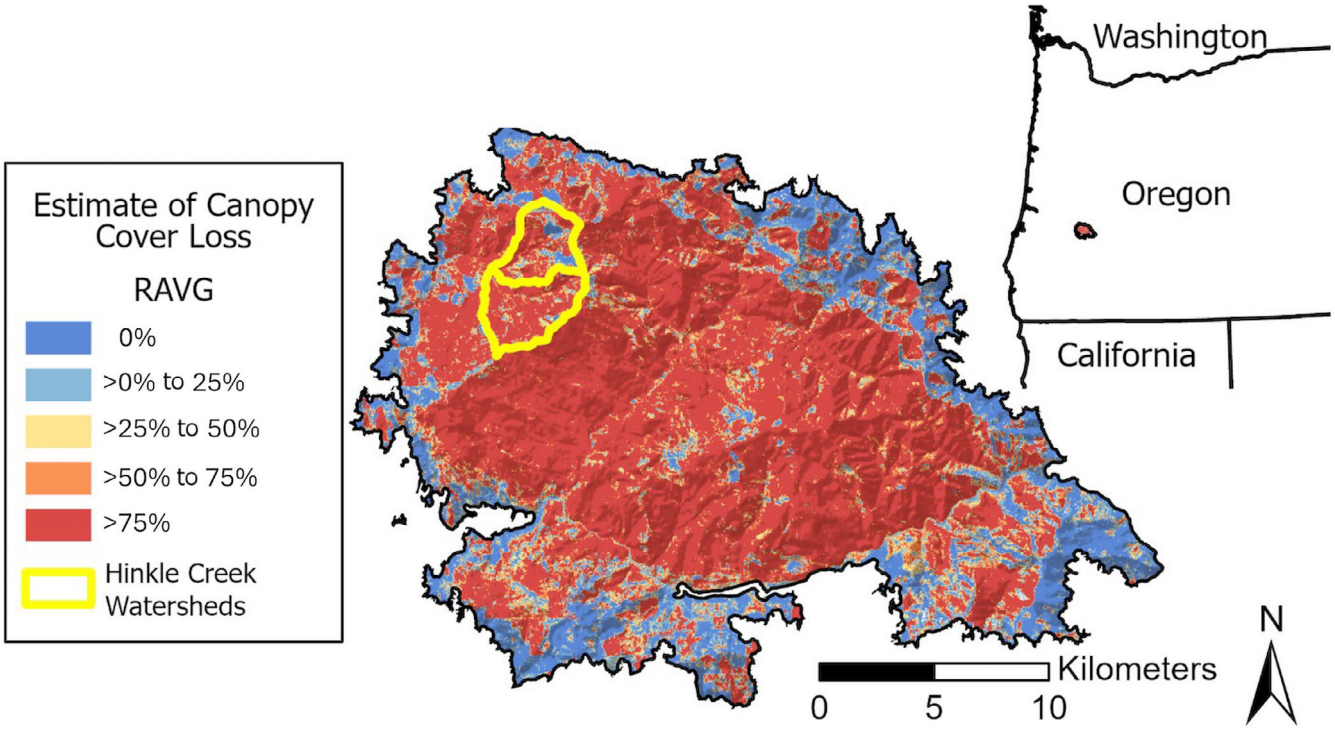


FIGURE 1 Map of the Hinkle Creek sub-basins within the Archie Creek Wildfire (2020) burn perimeter in western Oregon, USA. Burn severity was characterized by 5-class estimated canopy cover loss from the Rapid Assessment of Vegetation Condition After Wildfire (RAVG from USDA, https://burnseverity.cr.usgs.gov/products/ravg). Inset on the right: The Archie Creek Fire perimeter location in western Oregon.

watershed divide. Precipitation falls primarily as rain from November to April with intermittent snow in the winter, particularly at higher elevations. Hinkle Creek is a high-gradient system (mean ≥4%) with step-pool, forced pool, cascade, exposed bedrock, and riffle-run morphologies and the substrate is primarily mixed cobble (Bateman et al., 2016). There are naturally reproducing populations of four aquatic vertebrates in Hinkle Creek, including cutthroat trout, both anadromous (steelhead) and resident (Coastal rainbow trout) populations of *Oncorhynchus mykiss irideus* (hereafter "*O. mykiss*"), reticulate sculpin (*Cottus perplexus*), and Pacific giant salamanders (*Dicamptodon tenebrosus*). The extent of stream that each of these species inhabits varies along the mainstem. Cutthroat trout and Pacific giant salamanders were present through the entire mainstem in almost all years. The upper extent of reticulate sculpin across years ranged from approximately 2000 to 3000 m while the upper extent of *O. mykiss* ranged between approximately 1000 and 2300 m.

2001–2011 Hinkle Creek Paired Watershed Study

Data on stream fish were collected annually from both the North Fork and South Fork of Hinkle Creek from 2001 to 2011 as part of the Hinkle Creek Paired Watershed Study (HCPWS; Bateman et al., 2016; Berger & Gresswell, 2009; Ganio et al., 2005; Gerth et al., 2022; Kibler et al., 2013; Li et al., 2016). The goals of the original study were to quantify the effects of forest management activities on streamflow, stream temperature, suspended sediment, stream nutrients (nitrogen and phosphorus), aquatic habitat, and aquatic fauna (Figure 2). The catchment had been previously logged in the early- to mid-1900s. At that time, there were no requirements for stream buffers, resulting in stands being cleared down to the stream banks during the first harvest. The HCPWS took place about 60–80 years after the first timber harvest entries into this area and was, therefore, explore the effects of forest management on second- to third-rotation harvests. During these harvesting activities, management regulations required riparian buffers for fish-bearing streams, restricted clear-cut sizes, and better road conditions (Bateman et al., 2016; Kibler et al., 2013; Li et al., 2016).

In the original HCPWS, data on habitat and fish were collected from 2001 to 2005, prior to forest harvesting ("pre-treatment"), from both the North Fork and South Fork (although approximately 11% of the South Fork sub-basin was harvested in three mid-elevation—not near streams—cut blocks in the years proceeding this pre-harvest data collection period; Figure 2; Appendix S1: Figure S1, Table S1). After 5 years of monitoring, researchers implemented the first stage of the watershed

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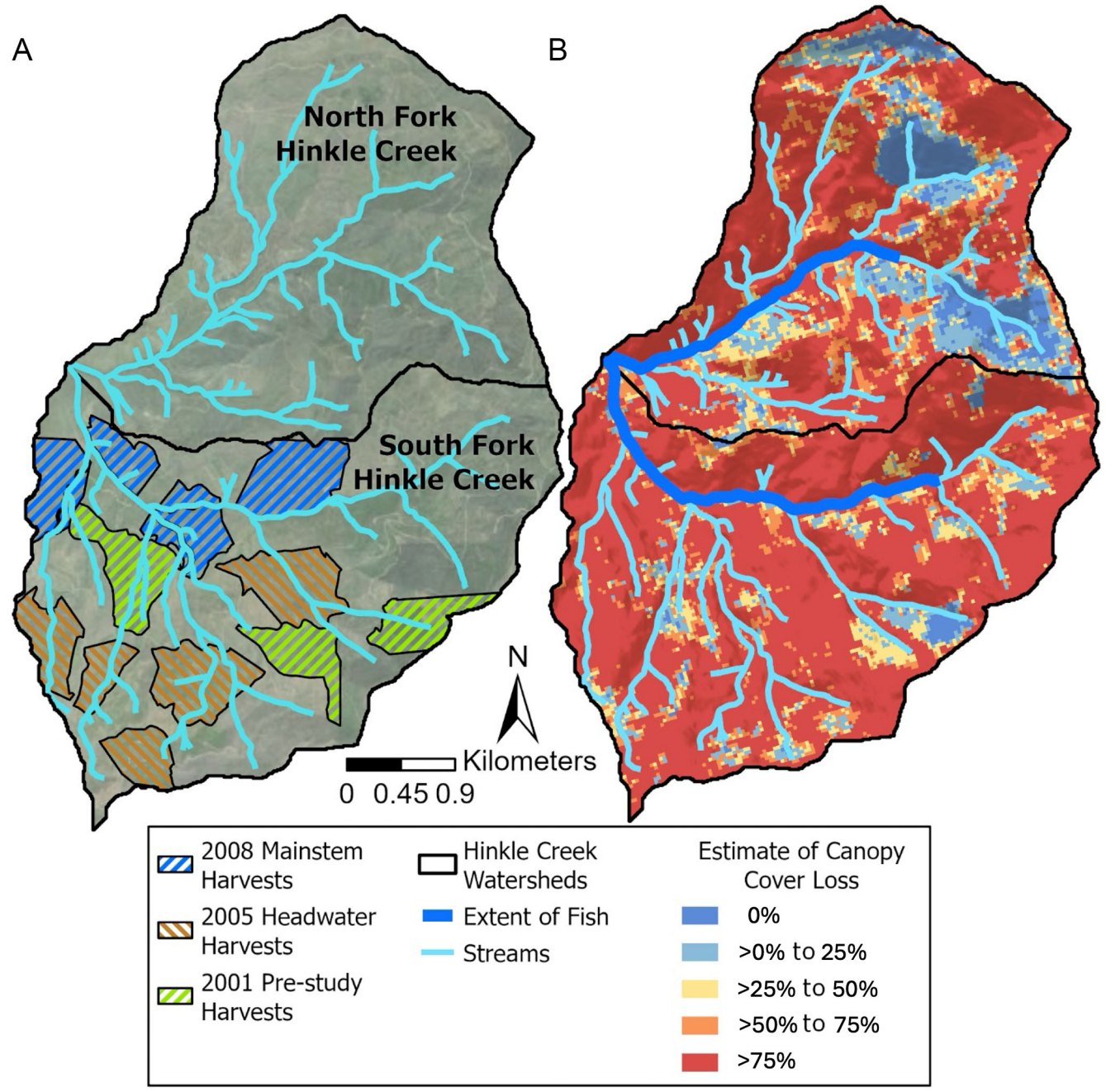


FIGURE 2 (A) The Hinkle Creek sub-basins and treatment harvests from the Hinkle Creek Paired Watershed Study (2001–2011). The North Fork was unmanaged, serving as a reference watershed, during the original study. The 2001 harvests occurred before stream monitoring began in summer 2001. (B) A map of the Hinkle Creek sub-basins and burn severity after the Archie Creek Fire (2020). The 5-class estimated canopy cover loss was collected from the Rapid Assessment of Vegetation Condition after Wildfire dataset (USDA). The dark blue line in this map represents the historic extent of fish in the mainstem of both sub-basins, although fish were also present in tributaries.

experiment between August 2005 and May 2006. This included five clear-cuts, totaling 154 ha (approximately 14% of the South Fork), at or above the known upper fish-bearing extent of tributaries draining SFHC. The North Fork drainage remained unharvested as a reference catchment throughout the HCPWS (Bateman et al., 2016, Kibler et al., 2013, Li et al., 2016). In 2008, the second stage of the project experiment (five more clear-cuts, totaling 114 ha—approximately 11% of SFHC) was implemented with management adjacent to the mainstem of SFHC and the fish-bearing reach of one of its tributaries. After this second stage of harvesting, data were collected for three additional years (2009–2011). Following the completion of the study in 2011, forest

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operations continued in SFHC and an additional 369 ha (approximately 34% of SFHC) were cut from 2014 to 2018.

During the original HCPWS, fish and habitat monitoring occurred annually at the end of summer (August–September) from 2001 to 2011. Data on water chemistry, discharge, sediment fluxes, and temperature were monitored throughout the year. Habitat data were collected using continuous surveys through the known extent of fish along the mainstems of NFHC and SFHC and along their fish-bearing tributaries (Bateman et al., 2016). Although the NF Hinkle Creek system remained unharvested during the paired watershed study, the lower mainstem of this stream was stocked with juvenile salmon during the first 2 years of the pre-treatment period (2001, 2002). There were no lasting effects as these fish emigrated within a year; however, the addition of these fish in those 2 years restricts comparisons in the fish response using the NF as a reference until 2003.

Archie Creek Fire—September 2020

In 2020, the Archie Creek Fire was one of five large wildfires that burned across the western Cascade Mountains of Oregon (Reilly, Norman, et al., 2022). The Archie Creek Fire burned more than 53,000 ha in the central Oregon Cascades. Nearly all the Hinkle Creek watershed was burned (approximately 1850 ha) with 44% of the area burning at moderate severity and 33% at high severity (Warren et al., 2022). More than 70% (1414 ha) of the Hinkle Creek watershed suffered >75% canopy cover loss and over 15% (308 ha) of the catchment experienced between 25% and 75% canopy cover loss (Figures 1 and 2; https://burnseverity.cr.usgs.gov/ravg/data-access). In SFHC, much of the vegetation in the watershed was lost due to the fire and within a year after the fire, nearly 179 ha (approximately 17% of SFHC) of the watershed was salvage logged (Appendix S1: Table S1). Because the entire Hinkle Creek watershed burned during the Archie Creek Fire, the NFHC could no longer serve as a clear reference watershed, and given logistical constraints and the loss of a paired watershed design, we focused post-fire data collection on the mainstem of SFHC.

Post-fire longitudinal summer stream temperature

In June 2023, we added Hobo TidBit V2 (Onset Computer Corporation) temperature sensors throughout the mainstem of SFHC to capture longitudinal variation in stream temperature following wildfire (Appendix S1: Figure S2). Overall, 22 stream temperature sensors were deployed along the mainstem with a spacing of approximately 250 m. Temperature sensors recorded temperature (in degree Celsius) every 15 min from July 1 through September 30. The mean of the daily maximum stream temperatures through this time period was used as our primary temperature metric for analyses.

Fish surveys

Across both pre- and post-fire, fish sampling surveys were conducted annually between early August and late September during low-flow conditions and following protocols established for the HCPWS. The methods for fish sampling during the pre-treatment period of the HCPWS and in the time after the headwater harvest in that study are detailed in Bateman et al. (2016). The same methods were applied in sampling the three additional years after the mainstem forest harvest period and during in the post-fire period. Briefly, all pools along the entire mainstem were identified during mid- to late-summer, prior to fish sampling. Then, during the fish sampling period, all salmonid fish were collected from every pool using single-pass electrofishing (300–450 v with DC current). This consisted of running the electrofishing a pool continually until no more fish were seen or moved by the electrofisher (sampling without block nets).

This single-pass pool census assessment method was evaluated in a 2005 study (Bateman et al., 2005) and was found to capture an average of ~78% of the estimated population of trout in the full reach (encompassing pools, riffles, glides, backwater, etc.) of a Coast Range stream, and ~74% of the estimated population of trout in the full reach of a western Cascades stream. We conducted a separate validation of the method for our post-wildfire assessment study at four sites in 2021 and at one site in 2023. We found a comparable degree of efficiency with single-pass pool-only surveys capturing 69%–77% of the total population estimate from within a study reach in the middle and upper portions of the watershed. We found lower efficiency in the larger, downstream portion of the mainstem, which we attributed to more backwater and non-pool habitat that was suitable for fish. Since error around estimates in this portion of the mainstem is due to fundamental habitat features, we assumed this error would be present in all surveys across all years and so comparisons across years before and after experimental treatments and wildfire remain valid—though inference about total abundance in upper reaches versus the lower mainstem were likely not as robust (validation assessment details in Ivie (2024)).

Due to changes in streamflow and morphology over time, the number of pools surveyed varied across all

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years. In the pre-fire survey period, the number of pools surveyed ranged from 245 to 307 along the mainstem of SFHC and from 182 to 242 along the mainstem of NFHC (Table 1). Mean size of pools also varied with pre-fire pool area in SFHC ranging from 9.42 to 12.79 in SFHC mainstem and from 8.37 to 10.77 in NFHC (Table 1). In the post-fire years, we identified pools following the sampling protocols laid out by Bateman et al. (2016) in the original HCPWS, but we fished fewer pools. We identified pools in 2022 as areas of slow-moving or still water which spanned approximately 90% of the wetted channel width, where mean pool depth was visually deeper than the rest of the stream, and there was a clear pool forming feature (Bateman et al., 2016). In many places, a "pool" was clearly identifiable; however, in other areas pools were challenging to identify and somewhat subjective, particularly during low-flow conditions. We sampled only 98 pools in 2022, but in this year, we were not able to fully census the mainstem (ending at meter 2772, approximately ¾ of the likely full distribution of fish; Appendix S1, Figure S3). Average pool size in 2022 was larger (12.33 m^2) than in all but one of the previous surveys (Table 1). We attributed the larger average size and smaller number of pools in part to missing portions of

TABLE 1 Annual pool survey data from all years in pre- and post-fire periods in NF Hinkle Creek (NFHC) and SF Hinkle Creek (SFHC). Max distance is the distance from the confluence of SFHC with NFHC where the last pool was fished in that year and also represents the upstream extent of fish (except in 2022 when the surveys were not completed through the upstream extent of fish due to logistical constraints).

Stream	Year	Disturbance period	No. pools	Mean pool area (m^2)	Total area sampled (m^2)	Distance sampled (m)	Mean August stream temperature (°C)	Mean August discharge ($m^3\ s^{-1}$)
North Fork Hinkle Creek	2003	Pre-harvest	242	8.55	2070	2682	15.5	0.008
	2004	Pre-harvest	234	9.33	2183	2722	15.4	0.019
	2005	Pre-harvest	182	8.37	1523	2628	15.2	0.014
	2006	Headwater harvest	210	8.95	1880	2685	14.3	0.009
	2007	Headwater harvest	224	8.43	1887	2770	14.5	0.008
	2008	Headwater harvest	242	8.41	2036	2804	14.9	0.013
	2009	Mainstem harvest	227	10.77	2444	2656	15.3	0.008
	2010	Mainstem harvest	228	8.62	1965	2812	14.4	0.015
	2011	Mainstem harvest	213	9.32	1985	2774	14	0.031
	2022[a]	Post-fire	...	...	...	...	19.6	0.020[a]
	2023	Post-fire	...	...	...	...	20.3	0.005[a]
South Fork Hinkle Creek	2003	Pre-harvest	278	11.71	3256	3770	15.2	0.024
	2004	Pre-harvest	290	12.79	3708	3492	15.3	0.045
	2005	Pre-harvest	295	10.17	3001	3567	14.9	0.029
	2006	Headwater harvest	286	10.46	2993	3555	13.9	0.033
	2007	Headwater harvest	268	9.42	2526	3595		0.027
	2008	Headwater harvest	248	9.75	2417	3497	14.5	0.041
	2009	Mainstem harvest	284	11.48	3262	3560	14.9	0.035
	2010	Mainstem harvest	245	10.29	2520	3626	14.2	0.052
	2011	Mainstem harvest	254	10.39	2639	3688	13.7	0.084
	2022[b]	Post-fire	98	12.33	1208	2772	18	0.051[a]
	2023	Post-fire	186	7.89	1467	3980	18.7	0.021[a]

Note: Mean August temperature and stream discharge for NFHC and SFHC collected at the downstream end of the stream, just before their confluence. Discharge estimates in 2022 and 2023 are based on discharge at the nearby Oregon Water Resources Department Calapooya Creek stream gage, which had a strong relationship with NFHC and SFHC gages in the pre-fire sampling period (Appendix S1: Figure S4).

[a]Discharge estimate based on Calapooya Creek gage station.

[b]For this year only, fish surveys did not reach the upper extent of fish in mainstem SFHC.

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the upper region of the system where pool sizes were smaller (Berger & Gresswell, 2009). However, the distance upstream could not fully account for the number and size of pools in 2022 sampling. We believed that conditions identifying a "pool" in 2022 may have been more stringent than those in previous years. Therefore, for our 2023 surveys, we adjusted our definition of a pool to allow for slightly less proportional wetted width coverage (Ivie, 2024). In addition, in 2023, we used multiple teams to increase survey efficiency and ensure we could reach the end of fish in SFHC (which also yielded more comparable crew effort relative to the original HCPWS). In 2023, we fished all pools along ~4000 m of the mainstem ($n = 186$), which extended through and beyond the historically fish-bearing portion of SFHC (Table 1).

In the pre-fire HCPWS, pool locations were determined relative to benchmark trees at established distances from key geomorphic features (e.g., stream confluences), ultimately yielding a distance estimate from the downstream confluence of NFHC and SFHC. Tree tags were lost in the wildfire. In the post-fire survey period, the distance of each pool along the mainstems of SFHC was determined using a measuring tape in combination with GIS distance measurements (locations determined using Avenza Systems, Toronto, ON) from established geomorphic features such as stream confluences that would not be affected by fire. At each pool, we quantified pool length and mean pool width (calculated from wetted widths measured at approximately ¼, ½, and ¾ pool length using a laser distance meter) to estimate pool surface area. We also measured maximum pool depth and outflow depth (cm).

Across all years, for all salmonid fish, total length (TL) and fork length (FL) to the nearest mm and mass to the nearest 0.1 g were recorded. All age-1+ salmonids were identified to species, but we did not distinguish resident rainbow trout from anadromous steelhead and referred to both groups as simply *O. mykiss*. Because species identification of newly emerged age-0 life stages is not possible in all cases, this group was broadly designated as young-of-year (YOY). The FL cutoff for YOY salmonids was 95 mm in 2022 and 85 mm in 2023, based on post hoc length frequency distributions of salmonids (Ivie, 2024). Length cutoffs for YOY from the pre-fire fish data were also determined using length frequency distributions of FL, resulting in unique length cutoff for age-0 trout each year determined by researchers in the HCPWS (Appendix S1: Table S2). In the pre-fire assessments, sculpin and salamanders in the pools were noted, but not captured or enumerated. In the post-fire period, salamanders and sculpin were collected and processed with the salmonids, but priority was placed on capturing salmonids in the pools to best match the HCPWS methods (Ivie et al., 2026).

Analysis of mean fish density and mean fish biomass density in pools

For analyses comparing North Fork and South Fork in the pre-fire period, we excluded 2001 and 2002 data because the mainstem of NFHC was stocked with a high density of juvenile salmon in those years (D. Bateman, personal communication), which can impact the dynamics of cutthroat trout and *O. mykiss* in this system. The post-fire fish sampling surveys were conducted in August in both 2022 and 2023 to best match the range of dates from the earlier HCPWS.

For each pool along both the SFHC mainstem and NFHC mainstem across all viable pre-fire years (2003–2011), we determined abundance density (in number of fish per square meter) per pool and biomass density (in grams of fish per square meter) per pool for cutthroat alone and for all salmonids together, which was a combination of cutthroat, *O. mykiss*, and YOY. Fish density and biomass density were used as the primary fish response metrics in the previously published assessment of fish response to the headwater harvest in the HCPWS. Abundance density was calculated in each pool as the number of individuals (cutthroat trout or all salmonids) caught in the single-pass electrofishing divided by the pool area, and biomass density was calculated as the summed biomass of all individuals (cutthroat trout or all salmonids) divided by pool area. We calculated the same abundance densities and biomass densities for each pool surveyed in the post-fire period (2022 and 2023) in SFHC. For each year, we calculated a mainstem mean abundance density and a mean biomass density of cutthroat trout or all salmonids. Annual data were binned into four disturbance periods: pre-harvest monitoring (3 years before experimental harvests: 2003–2005), headwater harvests (3 years following first experimental harvest: 2006–2008), mainstem harvests (3 years following second experimental harvest: 2009–2011), and post-fire (2 years following the Archie Creek Fire and subsequent salvage logging: 2022–2023). We will refer to the period after Archie Creek Fire simply as the post-fire period, but from 2020 to 2023, this watershed not only experienced impact of a severe wildfire, but also salvage logging, and other forest management operations, such as replanting and herbicide application, which all occurred outside of the riparian buffer zone.

To compare fish metrics across disturbance periods, we estimated means of means ("meta-means") for each disturbance period (pre-harvest, headwater harvests, mainstem harvests, and post-fire) using an ordinary least squares (OLS) regression model (Fish Response ~ Disturbance Period—1), implemented in R via the "lm()" function in the "*stats*" package (R Core Team, 2023). We

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first calculated the mean (± SD) of biomass and density for all pools in each year for both cutthroat and all salmonids. Before calculating annual means, we excluded one particularly high-leverage pool from 2023 in the analysis. This pool had a small surface area and held several large cutthroat trout, resulting in an abnormally high relative biomass value of 206.6 g m^{-2}. With this high-leverage pool included, the estimated mean values for 2023 were 0.50 fish m^{-2} and 13.51 g m^{-2}, but without the pool included the estimated values were 0.47 fish m^{-2} and 12.21 g m^{-2}. We averaged the annual means across each period and added period as a random effect in our models. After calculating the means for each individual year, we fit the OLS model to get meta-mean estimates for each disturbance period. We used residuals versus period and residuals versus year plots to check for independence and equal variance in the residuals, and a Q-Q plot to check for normality in the residuals and found that model assumptions were reasonably met. We further checked for temporal autocorrelation in the residuals by plotting partial autocorrelation functions for the first 11 years of data and did not find evidence of autocorrelation.

In assessing the effects of forest management on cutthroat trout and all salmonids along the mainstem during the pre-fire period of the original HCPWS, we calculated the difference between abundance density per pool (number of fish per square meter) and mean biomass density (biomass of fish per square meter; in grams per square meter) in SFHC and NFHC in each year from 2003 to 2011. To assess potential management effects on pool densities, we compared the mean difference in pool abundance or biomass densities between SFHC and NFHC in the two forest management periods relative to the pre-management period using an ANOVA with "significant" response at $p < 0.05$ and "moderately significant" responses at p between 0.05 and 0.1. We did not have a reference site in the post-fire period, and therefore our comparisons focus on overall meta-mean densities of cutthroat trout and all salmonids during the post-fire period relative to the three pre-fire periods, which encompass the range of variation seen in this system over 11 years.

Because annual climate conditions—particularly streamflow which integrates precipitation from the previous year—can affect overall fish abundance as well as relative densities in pools as surface area changes, we evaluated the relationship between summer baseflow discharge and stream salmonids to see if hydroclimate over the previous year could be a factor accounting for changes in our fish population metrics. For this assessment, we used mean August discharge as a proxy for relative annual summer baseflow, and we used mean adult cutthroat trout biomass density per pool in SFHC as our focal fish metric. In the pre-fire HCPWS, August baseflow discharge could be quantified directly in SFHC from a gage on the lower portion of the stream beginning in 2003. This gage was discontinued after the end of the HCPWS (end of 2011). The gage was severely damaged during the 2020 wildfire, and it therefore could not be used in our post-fire analysis, but fortunately, the Oregon Water Resources Department has been running a gage in nearby Calapooya Creek, which can be used to broadly estimate discharge patterns at SFHC in these two missing years (https://apps.wrd.state.or.us/apps/sw/hydro_near_real_time/display_hydro_graph.aspx?station_nbr=14320700). Calapooya Creek is the larger stream into which Hinkle Creek runs, and therefore streamflow conditions—particularly in summer—are highly correlated ($r^2 = 0.85$ for mean August discharge at SFHC gage versus Calapooya Creek gage from 2003 to 2011; Appendix S1: Figure S4), and a substantial portion of the area upstream of this gage was impacted by the Archie Creek Fire. Given the strong relationship between these two sites, we used mean August discharge at Calapooya Creek in 2022 and 2023 to estimate an approximate baseflow discharge conditions at SFHC in those 2 years. We broke the data into our four time periods (HCPWS pre-treatment at SFHC 2001–2005, HCPWS post-headwater harvest 2006–2008, HCPWS post-mainstem harvest 2009–2011, and post-fire 2022 and 2023) but more broadly analyzed the August baseflow discharge relative fish biomass relationship collectively for the full pre-fire period together. We then evaluated post-fire discharge and mean biomass density values relative to the pre-fire relationship.

Analysis of longitudinal patterns of cumulative fish density and biomass density

To assess the spatial variation and total relative density and biomass along the mainstem, we created cumulative longitudinal distribution profiles for all pre- and post-fire years. For this analysis, we again removed our outlier pool from 2023 to be more conservative with our post-fire estimates. To create the cumulative longitudinal distributions, we summed the per pool biomass and densities for all pools within 50-m bins through the mainstem and then created a cumulative function for the collective bins. We selected 50-m bins for a minimum of three pools in each distance bin, which reduced the relative influence of individual outlier pools and aligned with bin distances in the bootstrap analyses (see below). From the cumulative longitudinal distribution data, we calculated the mean of the total biomass and total density for both species groups (adult cutthroat trout and all salmonids) in

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each pre-fire sample year and period and compared those to the two post-fire years. Because we were not able to sample to the upstream extent of fish in 2022, the comparison for that year relative to the pre-fire period is considered conservative.

To draw further inferences on the longitudinal spatial distribution of trout biomass and density, we also normalized the cumulative longitudinal distributions relative to the total values for each year. After creating proportional distributions, we calculated the distance at which the distribution reached 25%, 50%, and 75% of the total value. This allowed us to assess how these spatial patterns shifted among years and therefore where the majority of biomass and density was each year within the mainstem.

Analysis of forest management responses

To contextualize forest management responses, we also created cumulative longitudinal distribution profiles for cutthroat trout and total salmonid biomass and density in the NFHC from 2003 to 2011, which was set up as the reference site for the initial Hinkle Creek study and created a before–after control-impact (BACI) study design for assessing responses to different harvest configurations in the basin (Bateman et al., 2016). We calculated the total cumulative values from the pre-fire data along the mainstem of NFHC and SFHC and compared the difference between these total values from pre-harvest years (2003–2005) to the differences from the years following the headwater (2006–2008) and mainstem harvests (2009–2011) in SFHC. As with the mean pool density analysis, due to high juvenile salmon stocking densities in 2001 and 2002 in NFHC, we excluded 2001 and 2002 from the NF-SF pre-fire comparisons. In assessing the post-management responses in the total age-1+ cutthroat trout density, total age-1+ cutthroat trout biomass, total salmonid density, and total salmonid biomass, we compared the means of differences among each of the three time periods with available data from both basins ($n = 3$ each for pre-harvest, headwater harvest, and mainstem harvest). To test for significant responses to the two treatment harvesting treatments in the HCPWS, we fit a linear model with the sub-basin differences and conducted contrasts between the estimated means of differences of the pre-fire periods using emmeans contrasts in R (Lenth, 2024).

Post-fire bootstrap assessment

To compensate for the lack of a reference site during the post-fire period, we used the 2001–2011 SFHC data to create bootstrapped estimates of cumulative longitudinal biomass and density data. We compared the bootstrapped data with the empirical cumulative longitudinal curves from the post-fire period. No juvenile salmon stocking occurred in SFHC, to our knowledge, so we used the full 5-year pre-harvest data for this analysis (2001–2005). Overall, this approach enabled us to assess whether the post-fire fish biomass and density values throughout the mainstem were within an estimated historical range of variation across the pre-harvest and post-harvest periods of the study.

To preserve the spatial structure of the original data in the bootstrapped curves, we first created a longitudinal dataset in which we separated the entire length of the primary fish-bearing portion of the mainstem SFHC (0–3600 m) into 50-m bins. Because of changing stream morphology across years, the number and size of pools along the stream varied over time during each of the study years from 2001 to 2011 and for the 2022 and 2023 study years. Details on how the matrix for the cumulative bins in the bootstrap analysis was created are provided in Ivie (2024). The bootstrap analysis was run over 2000 iterations, creating 2000 individual cumulative distributions against which the two post-fire surveys could be compared.

To further compare how biomass and density accumulated in different portions of the mainstem of SFHC, we assessed the bootstrapped cumulative curves within stream segments. We used four stream segments defined in the original HCPWS as potentially biologically meaningful stream segments influenced by tributary junctions: Segment 1, 0–800 m; Segment 2, 801–1500 m; Segment 3, 1501–2550; and Segment 4, >2551. To remove the influence of downstream segments on cumulative longitudinal distribution profiles, we calculated within-segment cumulative totals for biomass and density. We did this for all 2000 iterations of the bootstrapped data and the two observed post-fire years. For each segment, we then determined the number of total values from the bootstrapped data which were less than the observed post-fire values to get a sense of how extreme the observed post-fire values are compared to what we would expect based on the historical variation.

RESULTS

Longitudinal summer stream temperature patterns

The longitudinal stream temperature profile during the post-fire period in summer 2023 showed a steady increase in daily mean and daily maximum stream temperature in the downstream direction (Appendix S1: Figure S5). At the most downstream temperature sensor, daily maximum stream temperatures between July 1 and September 30 ranged from

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13.2 to 27.0°C with a mean of 21.3°C. Daily mean temperature at the most downstream site in summer 2023 ranged from 12.3 to 22.1°C with a mean of 17.4°C. At the most upstream site in SFHC, the daily maximum stream temperatures ranged between 11.8 and 23.2°C (mean = 18.6°C) while daily mean temperatures ranged between 11.1 and 19.3°C (mean = 15.4°C). Tributaries brought in cooler water resulting in a decrease in stream temperature in the mainstem, which dissipated with distance downstream from the tributary confluence (Appendix S1).

Trout mean pool biomass and mean pool density comparisons

During the original HCPWS, the pre-harvest period had the lowest mean fish biomass and abundance in pools of SFHC relative to the two post-harvest periods (Figure 3). Although the meta-mean estimate of cutthroat trout biomass in pools in the headwater harvest period (3.5 g m^{-2}) was 33% greater than that in the pre-harvest period (2.0 g m^{-2}), when evaluated relative to the NFHC reference catchment, these differences are not as noteworthy because densities and biomass of cutthroat trout also increased in the reference catchment during the headwater harvest survey period (Table 2; Appendix S1: Figure S6). For cutthroat trout, the mean difference in meta-mean fish density and biomass in pools of the mainstem streams of SFHC and NFHC was not significantly different between the pre-harvest period of 2003–2005 and the headwater harvest period (2006–2008) ($p > 0.35$; Appendix S1: Table S3). Given the life history of anadromous *O. mykiss* in this region, returning adults are not expected to be found in the headwater reaches in summer. Consistent with this expectation, we found no returning adult sea-run (steelhead) *O. mykiss* in any surveys.

In considering the second treatment in the HCPWS, (the mainstem harvest period), the meta-mean cutthroat trout pool biomass per square meter over the 3 years after mainstem harvest in SFHC was 3.9 g m^{-2} (53% greater than the pre-harvest period; Table 2). Similarly, cutthroat meta-mean of abundance density estimates following

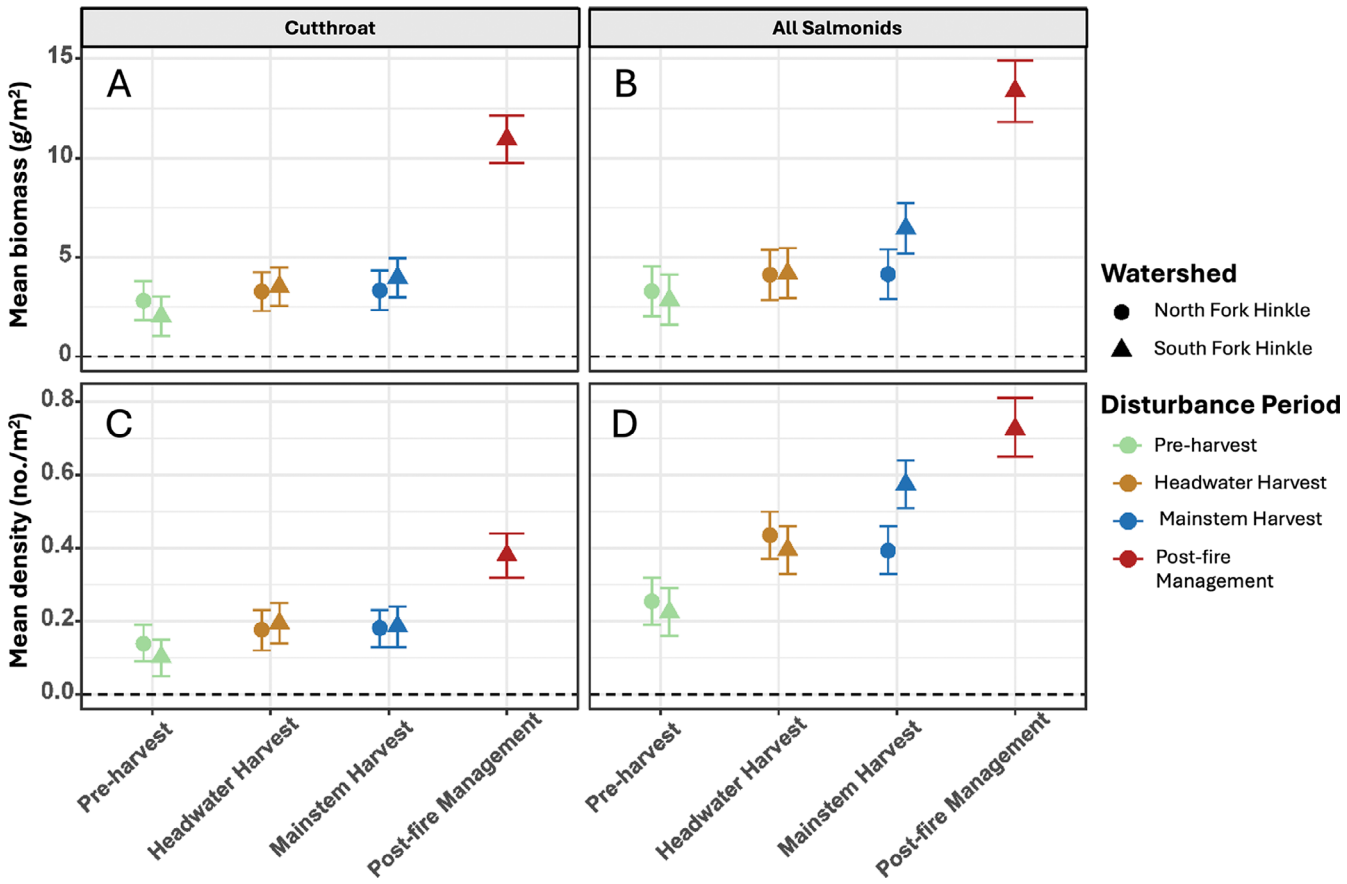


FIGURE 3 Plots of the estimated meta-means of trout biomass and density in pools of both North Fork and South Fork Hinkle Creek during each of the four time periods in our study (pre-harvest monitoring $n = 3$ years, headwater harvests $n = 3$ years, mainstem harvests $n = 3$ years, and post-fire $n = 2$ years). Meta-means were estimated using an ordinary least squares model. (A) Cutthroat biomass per pool, (B) relative all salmonid biomass per pool, (C) relative cutthroat density per pool, and (D) relative all salmonid density per pool. All salmonid estimates include age-1+ cutthroat trout, age-1+ *O. mykiss*, and young-of-year salmonids. Error bars represent 95% CI.

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TABLE 2 Estimated mean trout biomass and density per pool. Meta-mean estimates and 95% CI of biomass and density of age-1+ cutthroat trout and all salmonids (age-1+ cutthroat trout, age-1+ *O. mykiss*, and young-of-year salmonids) per pool area in the North and South Forks of Hinkle Creek, Oregon, USA.

			Cutthroat trout, CI			All salmonids, CI		
Response variable	**Watershed**	**Disturbance period**	**Mean**	**Lower**	**Upper**	**Mean**	**Lower**	**Upper**
Biomass per pool (g m^{-2})	North Fork	Pre-harvest	2.8	2.2	3.5	3.3	2.7	3.9
		Headwater Harvests	3.3	2.6	3.9	4.1	3.5	4.7
		Mainstem Harvests	3.3	2.7	4.0	4.1	3.6	4.7
	South Fork	Pre-harvest	2.0	0.7	3.4	2.9	1.0	4.7
		Headwater Harvests	3.5	2.2	4.9	4.2	2.4	6.0
		Mainstem Harvests	4.0	2.6	5.3	6.5	4.7	8.3
		Post-fire Management	11.0	9.3	12.6	13.4	11.2	15.6
Density per pool (fish m^{-2})	North Fork	Pre-harvest	0.1	0.1	0.2	0.3	0.2	0.3
		Headwater Harvests	0.2	0.1	0.2	0.4	0.4	0.5
		Mainstem Harvests	0.2	0.1	0.2	0.4	0.3	0.5
	South Fork	Pre-harvest	0.1	0.0	0.2	0.2	0.2	0.3
		Headwater Harvests	0.2	0.1	0.2	0.4	0.3	0.5
		Mainstem Harvests	0.2	0.1	0.2	0.6	0.5	0.6
		Post-fire Management	0.4	0.3	0.4	0.7	0.6	0.8

mainstem harvest (2009–2011) in SFHC was 0.2 fish m^{-2} (90.0% greater than that in the pre-harvest period). As with the headwater harvest period, the NFHC biomass per square meter and densities were also greater during this second harvest period than during the pre-harvest period; however, for biomass per in square meter in particular, the reference NFHC increases were smaller than those seen in SFHC pools (Figure 3). The analysis of the meta-mean differences between NFHC and SFHC indicated a significant increase in cutthroat trout biomass per in square meter following mainstem harvest ($p = 0.007$). Interestingly, the meta-mean for cutthroat trout pool density differences between NFHC and SFHC between the pre-harvest and mainstem harvest periods indicated no significant change ($p = 0.52$), suggesting that during the period following mainstem harvest in SFHC, fish were larger, but not more numerous.

In our analysis of all salmonids (including cutthroat trout, *O. mykiss*, and all YOY salmonids together), we also observed greater densities and biomass per square meter in pools of SFHC in the post-harvest periods relative to the pre-harvest period (Figure 3). However, as with cutthroat trout, when normalized to changes in NFHC through time, there were no clear headwater harvest treatment effects on total salmonid density or biomass density per pool in the mainstem of SFHC ($p > 0.5$; Appendix S1: Figure S6, Table S3). In the period following mainstem harvest on SFHC, results for total salmonids were similar to the cutthroat trout response, with greater and "moderately" significant (p between 0.05 and 0.1) increases in the difference between NFHC and SFHC total salmonid biomass in pools after mainstem harvest ($p = 0.055$). The abundance of all salmonids was also greater after mainstem harvest, with an increase in NFHC and SFHC differences that was also moderately significant ($p = 0.096$). This difference in fish density response between cutthroat trout and total salmonids is likely attributable to responses in juvenile (YOY) fish.

Because the NFHC also burned in the Archie Creek Fire, we did not have a post-fire reference to assess relative responses. However, we can compare the post-fire period relative to the pre-harvest and post-harvest periods (including both the headwater and mainstem harvests) to assess post-fire response values relative to variations in biomass and abundance seen over 9 years of data collection. This comparison indicated that the post-fire period had the highest pool biomass per square meter and pool abundance per square meter for cutthroat trout and all salmonid fishes (Figure 3; Appendix S1: Figure S6). The estimated post-fire meta-mean included 2 years that represented a summer with higher baseflow discharge (2022) and a summer with lower baseflow discharge (2023). The meta-mean for cutthroat biomass per square meter pools of SFHC (11.0 g m^{-2}) over these 2 years was nearly three times greater than the meta-mean from the pre-harvest period and one and a half to two times greater than the mainstem and headwater periods in this stream, respectively (Table 2). Similarly, the mean

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cutthroat density in pools during the post-fire period (0.4 fish m^{-2}) was 149.0% greater than that in the pre-harvest period and 90.0% greater than that in both headwater and mainstem harvest periods. Further, for total salmonids, the meta-mean of all salmonid densities in pools during the post-fire period was 320.9% greater than that in the pre-harvest period, 225% greater than that in the headwater harvest period, and 110% greater than that in the mainstem harvest period.

In evaluating adult cutthroat trout biomass density relative to annual summer baseflow in SFHC, we found a clear positive relationship in the pre-fire study period ($r^2 = 0.6$; Figure 4). Estimated mean August discharge in the two post-fire years included an unusually high-flow year (2022) and an unusually low-flow year (2023) (Appendix S1: Figure S7). A statistical analysis could not be run on just two points, but there is clearly greater biomass density of cutthroat trout per unit discharge in the two post-fire years relative to the pre-fire period. In the post-fire period, 2022 (the higher flow year) had relatively higher biomass density of cutthroat trout, and 2023 (the lower flow year) had relatively lower biomass density of cutthroat trout, thereby suggesting a similar relationship to that of the pre-fire years, however with a notable shift up in the intercept along the *y*-axis of cutthroat trout biomass density.

Longitudinal patterns of cumulative biomass and density

The cumulative longitudinal distribution profiles of relative cutthroat trout biomass per square meter and abundance per square meter in pools varied across all years in SFHC (Figure 5). Total cumulative values for cutthroat biomass were highest in the two post-fire years, despite incomplete surveys in 2022 (Appendix S1: Table S4). The total pool biomass per square meter of cutthroat trout was lowest in the pre-harvest monitoring years in SFHC. Total cumulative cutthroat trout density in 2022 (38.9 fish m^{-2}) was the third highest where data ended at the 2800-m bin and despite only extending to 2700 m, the cumulative cutthroat trout density estimate in 2022 was still the second highest total at 3500 m from the other surveys (2008: 68.2; 2023: 57.1 fish m^{-2}). In 2023, the cumulative number of fish per square meter in pools for cutthroat trout was greater than most other years (except 2008) from about meter 3000 onward, and 2023 had the highest total cumulative density at the end of fish (68.5 fish m^{-2}). All salmonid biomass in SFHC showed more consistent distributions and total cumulative values across years and within disturbance periods (Figure 6). When including cutthroat trout, *O. mykiss*, and age-0 salmonids, 2011 showed rapid accumulation of fish biomass

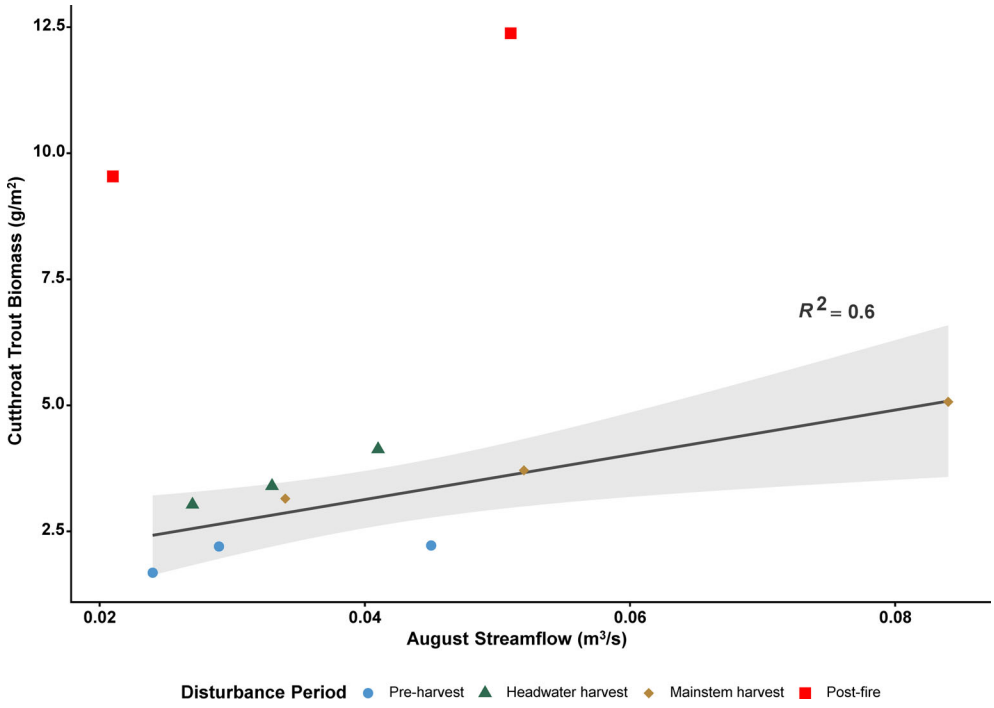


FIGURE 4 Relationships between mean discharge in August (the period during or shortly before fish sampling each year), and cutthroat trout biomass density per pool in South Fork Hinkle Creek from 2001 to 2011 (gray represents 95% CI). Data are broken down by color into four time periods: pre-treatment (2001–2005), headwater harvest (2006–2008), mainstem harvest (2009–2011), and post-fire period (2022, 2023). No analyses were done on the post-fire period as it only included two points.

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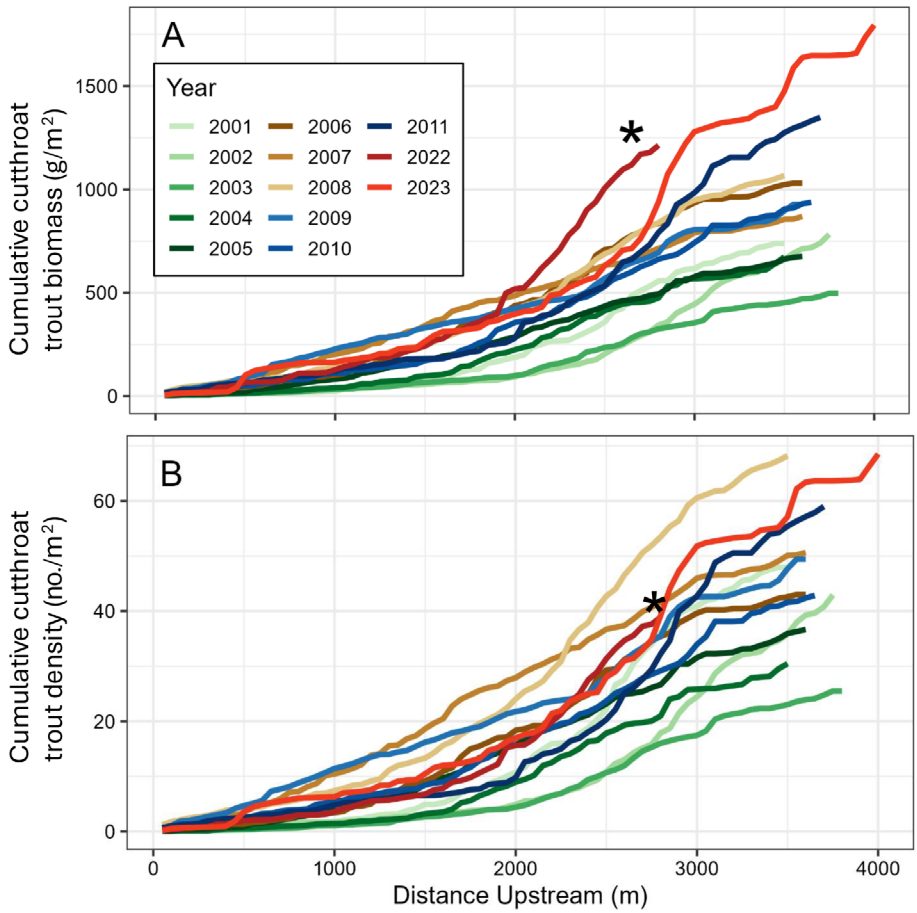


FIGURE 5 Cumulative longitudinal distribution profiles of age-1+ cutthroat trout (A) cutthroat biomass and (B) density per meter squared in pools through the mainstem of South Fork Hinkle Creek. Fish sampling in 2022 stopped before the upper extent of fish and is reflected by the end of this line at 2800 m and the asterisk (*) on the figure. Lines for all study years are grouped by disturbance period: pre-harvest monitoring (green), headwater harvests (brown), mainstem harvests (blue), and post-fire (red).

and had the highest total cumulative value in SFHC (2264.9 g m^{-2}). Similar to the cumulative distributions for cutthroat trout biomass, the 2022 all salmonid cumulative value was the second highest in SFHC even though it ended at the 2800-m bin (1453.1 g m^{-2}), and the 2023 value became the second highest value after the 2800-m bin (total cumulative value = 2240.7 g m^{-2}). All salmonid density also showed similarities within disturbance periods. Although for cutthroat trout, the total cumulative fish per square meter in SFHC pools was among the highest values, the total cumulative salmonid density for 2022 was among the middle to lower values (ranked sixth across the total 13-year data set) at the 2800-m bin (70.0 g m^{-2}). The total cumulative density of all salmonids for 2023 (138.7 g m^{-2}) was ranked 10th among all years and was less than the total cumulative density of salmonids in all three of the mainstem harvest years in SFHC.

Normalizing for total abundance and biomass to assess proportional longitudinal cumulative profiles of cutthroat trout along the mainstem, we found considerable variation interannually but there were no clear links to any disturbance period, including fire (Appendix S1: Figure S8). Years 2007 and 2010 had much higher cutthroat trout relative biomass per square meter lower in the system while in 2022, 2011, and 2023, fish biomass per square meter was lower in the areas further downstream but had a greater proportion of the population in the upper reaches of the system. When considered proportionally, the longitudinal distribution of cutthroat trout mass in 2023 aligned the most with the pre-harvest years and 2011. The same trends were seen with proportional cutthroat trout density. The proportional distribution of biomass and density for all salmonids followed relatively similar patterns to those of cutthroat trout alone (Appendix S1: Figure S9). Notable outliers were biomass per square meter accumulation in years 2007 and 2009, which reached 25% and 50%, respectively, of the total biomass, which is much lower in the system than in other years (Appendix S1: Table S5). In contrast, the pre-harvest years and 2023 had a greater proportion of captured fish further up in the system and had the furthest upstream distances at which 50% and 75% of total

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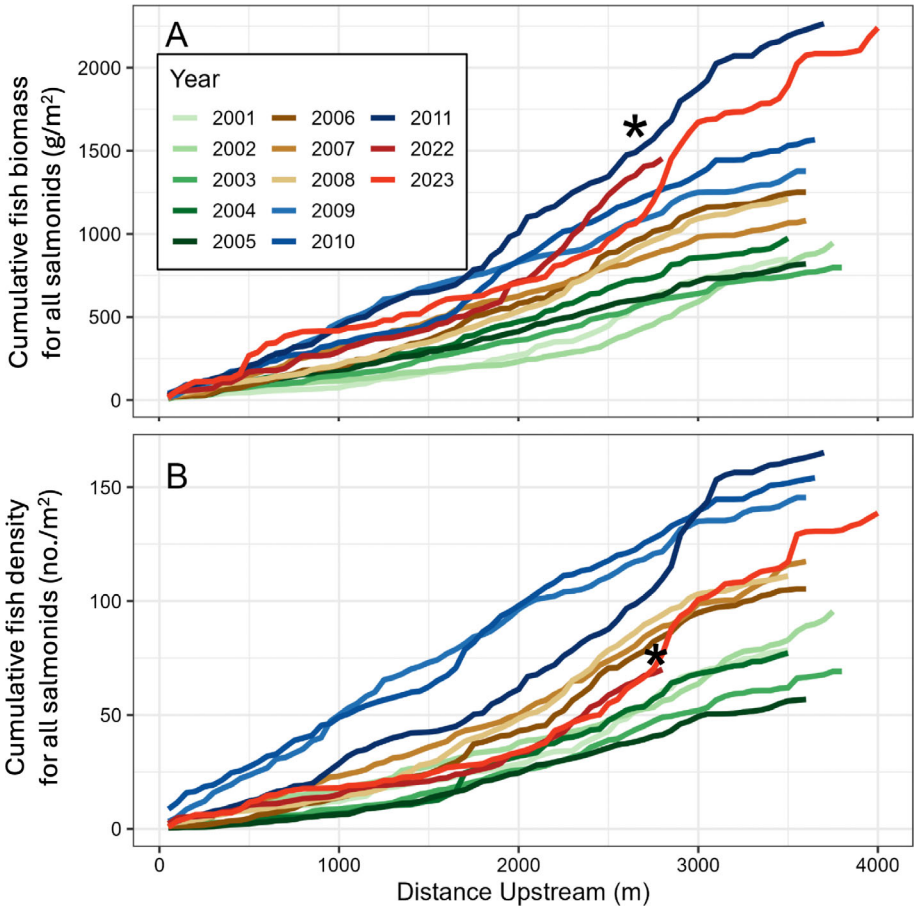


FIGURE 6 Cumulative longitudinal distribution profiles for all salmonids of (A) biomass and (B) density per meter squared in pools through the mainstem of South Fork Hinkle Creek. Fish sampling in 2022 stopped before the upper extent of fish and is reflected by the end of this line at 2800 m and the asterisk (*) on the figure. Lines for all study years are grouped by disturbance period: pre-harvest monitoring (green), headwater harvests (brown), mainstem harvests (blue), and post-fire (red).

captured fish biomass accrual occurred. For salmonid density, most years followed a similar pattern of a gradual proportional increase, except 2009 and 2010 had a high proportion lower in the mainstem and 2023 had a lower proportion lower in the system.

Pre-fire sub-basin comparisons

In assessing total cumulative biomass and abundance per square meter along the mainstem of SFHC relative to NFHC, we found that differences between sampling periods were in part attributable to overall differences between years. When corrected for cutthroat trout and salmonid total biomass and total densities in the NFHC, there was a relative increase in fish metrics in the two post-harvest periods, on average, particularly after harvests adjacent to the mainstem (Figure 7; Appendix S1: Figure S10). However, the mean differences between NFHC and SFHC during the pre-harvest period were not significantly different from the mean differences in the two post-harvest periods for cutthroat trout biomass and abundance ($p = 0.09$–0.85). For all salmonids, similarly, while there were greater biomass and abundance estimates in SFHC in the post-harvest periods, when corrected for the NFHC sites, the mean differences were not significantly greater after treatment than the pre-harvest periods ($p > 0.05$; Appendix S1: Table S6).

Pre-fire variation: SFHC Bootstrap analysis

Given that there was no reference site available in the post-fire period, we used our bootstrapping analysis to evaluate the mainstem totals from 2022 and 2023 relative to the potential variation in this system prior to fire but under the common forest management disturbances that have recently dominated these systems. The bootstrap analysis showed a wide range of potential variation in the pre-fire period for all four fish metrics, yet the total

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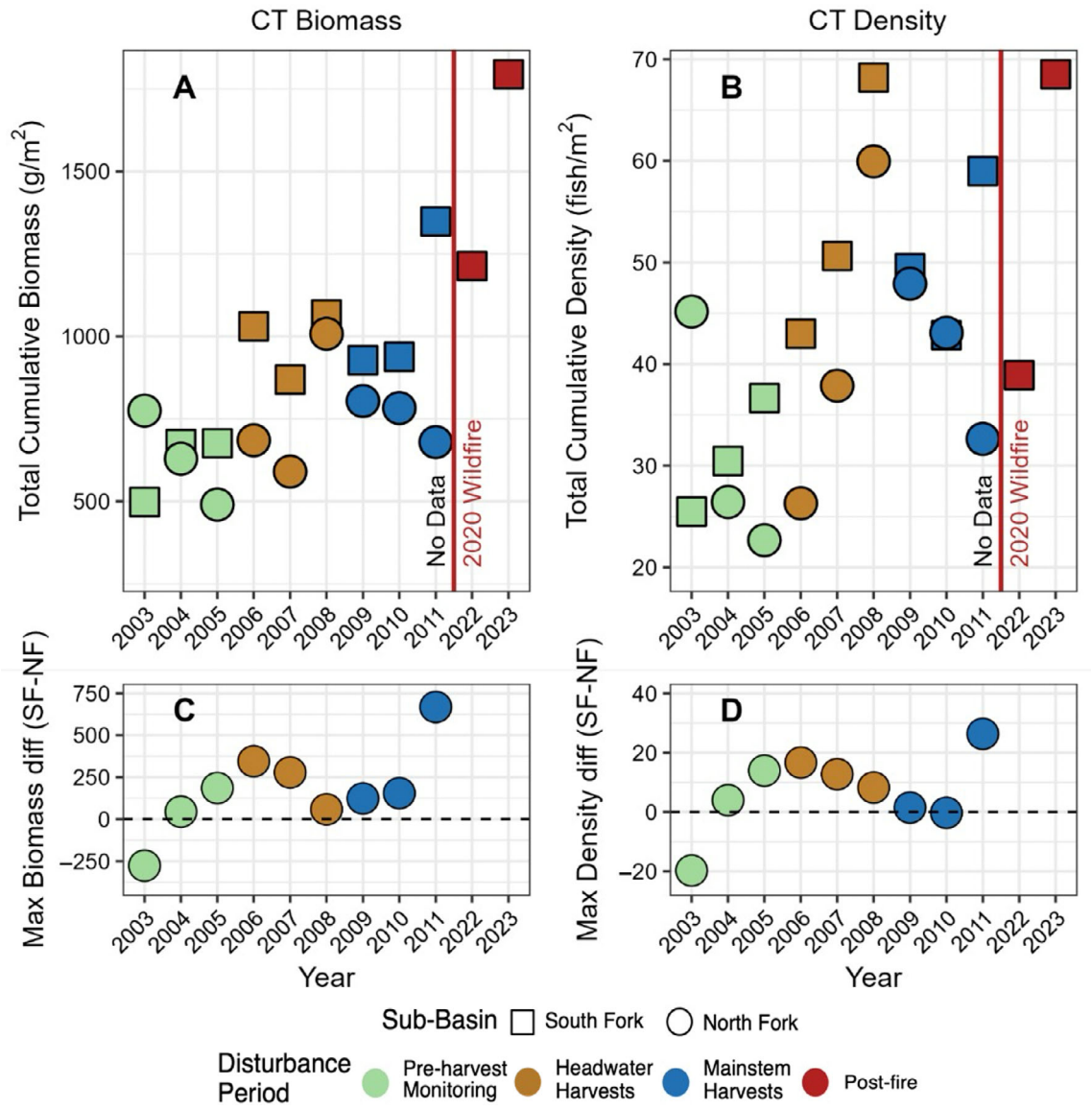


FIGURE 7 Cutthroat trout sub-basin total cumulative biomass and density. (A) Total cumulative biomass and (B) total cumulative abundance (density) of age-1+ cutthroat trout in South Fork Hinkle Creek (SFHC) and North Fork Hinkle Creek (NFHC). SFHC was the treatment site and NFHC was the reference site in the pre-fire forest management study. (C) Differences in total cumulative biomass between NFHC and SFHC and (D) differences in total cumulative abundance (density) between NFHC and SFHC. Because both catchments burned in 2020, no post-fire data were collected from the NFHC, and so bottom panels do not include values for 2022 and 2023.

cumulative cutthroat biomass per square meter for 2022 and 2023 was >100% of the bootstrap iterations from all pre-fire years (Figure 8). The post-fire total cumulative cutthroat density was also greater than in most iterations, but it was not as far outside the estimated range of variation from the pre-fire years. Total cumulative cutthroat trout density in 2022 was >81.8% of the pre-fire cumulative distribution iterations and 2023 was >91.3% of the iterations. Within stream segment 3 (1525–2550 m), the total cumulative values for 2022 cutthroat biomass per square meter and density were >100% and 87.65% of the cumulative totals from the bootstrapped data, respectively (Table 3). However, in 2023, cumulative cutthroat biomass per square meter and density were close to or <50% of the bootstrapped data for each of the first three stream segments, but cumulative biomass and density within the fourth stream segment (>2550 m) were >100% of the bootstrapped data. These results suggest that cutthroat trout responses to the fire were much more pronounced in the upper reaches—exceeding previous measured variation. However, in the lower sections of the mainstem, the biomass and abundances during the post-fire period were within the range of variation from previous disturbances in these systems.

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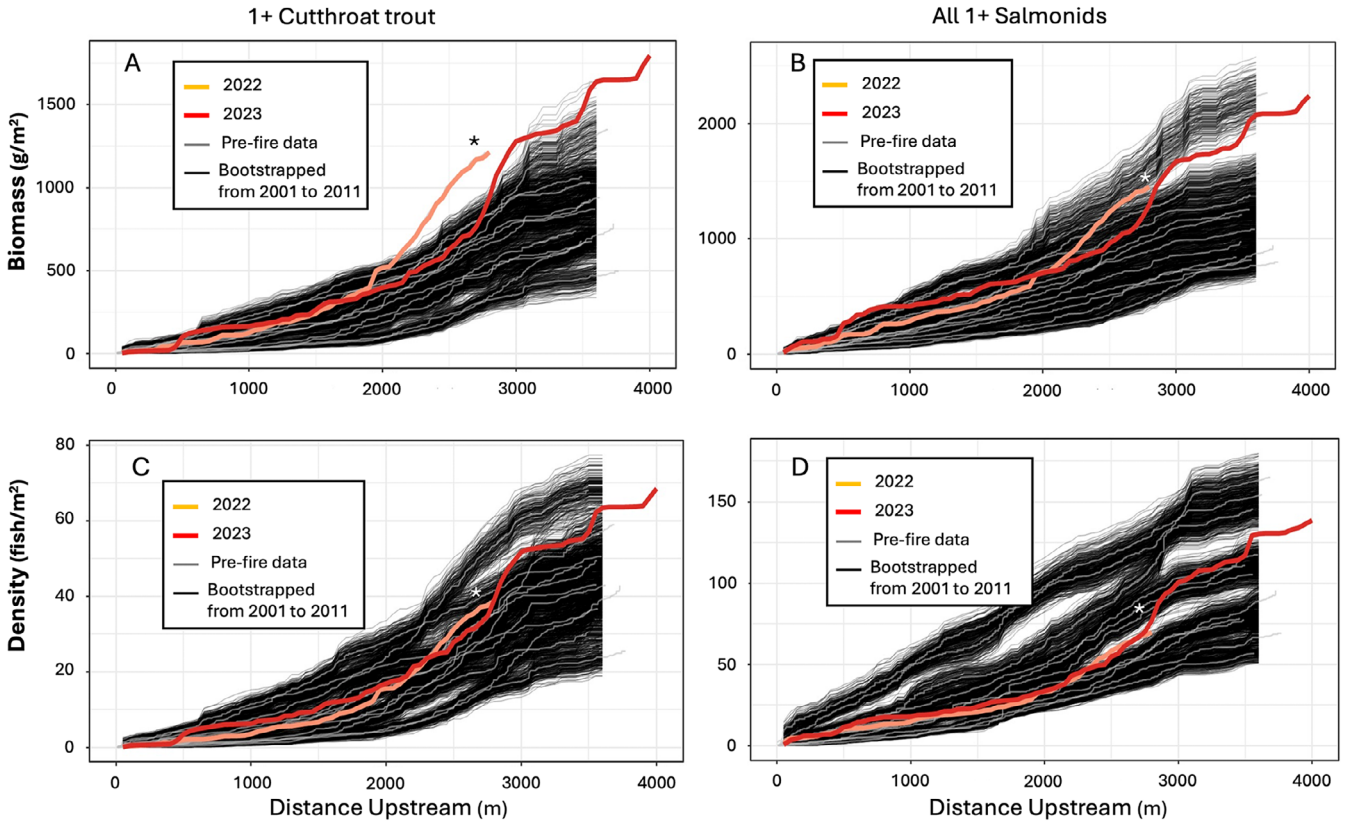


FIGURE 8 Empirical data and bootstrapped data for cumulative longitudinal distribution profiles of (A) biomass and (C) abundance (density) for age-1+ cutthroat trout and (B) biomass and (D) abundance (density) for all age-1+ salmonid fish in pools along the mainstem of South Fork Hinkle Creek. Observed post-fire years, 2022 and 2023, are in orange and red, respectively. Observed pre-fire years are in gray, and estimated range of variation from 2000 bootstrapped cumulative distributions from the pre-fire data is in black. The asterisk (*) indicates the end of 2022 fish sampling, but *not* the upstream extent of fish in that year.

TABLE 3 Within-segment totals of relative biomass and relative density within pools for age-1+ cutthroat trout and all age-1+ salmonids from the observed post-fire data (2022 and 2023). Observed value contextualized as a percent of the 2000 bootstrapped within-segment totals that were less than the observed totals in the post-fire years.

	2022				2023			
Stream segment	Total mass (g/m^2)	Percent below	Total density ($fish/m^2$)	Percent below	Total mass (g/m^2)	Percent below	Total density ($fish/m^2$)	Percent below
Cutthroat								
1 (0–800 m)	111	77	2.96	51	160	37	6.05	54
2 (801–1500 m)	242	40	6.77	0	265	2	10.47	43
3 (1501–2550 m)	1053	100	33.18	87	662	0	29.02	0
4 (2551–3600 m)	0.0	0	0.00	0	1638	100	63.41	100
Salmonids								
1 (0–800 m)	265	74	13.3	55	412	38	17.7	3
2 (801–1500 m)	428	0	20.9	0	556	24	24.2	0
3 (1501–2550 m)	1281	91	60.7	43	998	0	56.8	0
4 (2551–3600 m)	0	0	0	0	2075	100	130.4	100

The range of potential pre-fire variation for all salmonids was also wide. Total cumulative biomass per square meter was >91.8% of the bootstrapped data at the 2800-m bin in 2022 and 92.1% of the bootstrapped data at the 3600-m bin for 2023. As with cutthroat trout, total cumulative salmonid density was not as different from the

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bootstrap iterations as was total biomass per square meter (Figure 8). Cumulative salmonid density in 2022 was >45.5% of the bootstrap iterations and 2023 was >72.8% of the iterations (Table 3). In 2022 and 2023, total salmonid accumulations were slightly different relative to the bootstrapped iterations at the stream segment scale. In 2022, in contrast to cutthroat trout alone, total salmonid biomass per square meter accumulation in lower and middle sections of the mainstem were notably larger than most pre-fire accumulation iterations with segments 1 and 3 having cumulative biomass per square meter values that were higher than 74% and 91% of the bootstrapped data, respectively. In 2023, total cumulative biomass per square meter in stream segments 1–3 was lower than most of the bootstrapped data. However, as in 2022 and as with CCT alone (and largely driven by cutthroat trout in this upper section), segment 4 had greater cumulative biomass and density than all bootstrapped iterations.

DISCUSSION

During the first 2 years after a large, high-severity wildfire (and post-fire salvage), we observed substantially greater biomass density (in grams per square meter) and abundance density (in number per square meter) of cutthroat trout and all salmonids along the mainstem stream of a headwater catchment in western Oregon, when compared to 11 years of pre-fire data from that system as it underwent forest management. We also found that cutthroat trout and all salmonid biomass density and abundance density had stronger responses following wildfire in the upper reaches of the mainstem where maximum daily stream temperatures did not warm as much relative to the lower mainstem. In the pre-fire data period, we observed substantial variation in the total biomass density, abundance density, and longitudinal distribution of cutthroat trout and all salmonids both before and after forest management. Forest management resulted in notable relative increases in salmonid biomass density in pools following the streamside (with buffers) harvest period, but increases in fish biomass density and abundance density following wildfire were much more substantial. Overall, our results indicate that cutthroat trout and *O. mykiss* not only persist, but may potentially experience a short-term increase in overall biomass in headwater streams of managed landscapes after wildfire. Our results are important given that climate change and land management legacies have caused shifts in wildfire regimes leading to increases in the occurrence of large, high-severity wildfires in many regions across the planet, including the western United States. As in our case-study system, in many landscapes, these fires are also occurring in forests with a legacy of historic forest management or which are currently being managed for forest products.

Cutthroat trout and *O. mykiss* responses to forest management

In our study, data from the harvested watershed, SFHC, suggested a moderate increase in biomass per square meter and density of fish in pools after the headwater harvests relative to the pre-harvest period. The data from SFHC alone also suggested a further and more substantial increase after forest harvesting activities along patches of the mainstem. However, surveys from the unharvested, reference streams in NFHC enable us to account for annual variation in fish abundances and biomass across the pre-harvest and post-harvest time periods, and from this, it appears that the pre-harvest period was a time of lower fish abundances across both of these systems. Summer baseflow and associated climate conditions in the preceding year was a potentially important factor accounting for annual variation as cutthroat trout biomass densities in pools were positively related to mean August discharge in each year during the prefire period. However, given the proximity of NFHC to SFHC, it is likely that these climatic drivers affected both systems comparably, and so a focus on changes in the difference between streams in the BACI analysis ideally accounts for this. Indeed, while we observed increases in abundance and biomass densities of cutthroat trout and all salmonids in pools after harvests (in both periods) in SFHC, the normalized increases were more muted. The increases in relative abundance and relative biomass densities of cutthroat trout and all salmonids following the mainstem harvest were statistically different from the changes in NFHC over the same time period. However, changes were not statistically different in SFHC during the headwater harvest management period when evaluated in the BACI context.

Previous analysis of SFHC response to headwater harvests in the HCPWS assessed headwater tributaries (all streams but the mainstem) and the whole catchment (mainstem plus tributaries) (Bateman et al., 2016). In the earlier study, the difference in mean cutthroat trout biomass between tributaries with headwater harvests and control tributaries increased following harvest from -0.06 g m^{-2} before harvest to 1.48 g m^{-2} after harvest. However, at the whole catchment scale the change in difference after headwater harvest was smaller and did not yield a statistically significantly difference from pre-harvest estimates. The Bateman et al. (2016) study did not explicitly assess the mainstem alone, which was the

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focus of our analysis, but our results are generally consistent given the lack of significant response at the whole-stream scale.

The small increase in biomass density in SFHC following harvest along the mainstem of SFHC (with buffers) was consistent with observations from a similar study in the Alsea watershed in the Oregon Coast Range assessing effects of contemporary forest harvest on cutthroat trout (Bateman et al., 2018). Further, our observations were also consistent with results from a review by Mellina and Hinch (2009), which found that if forests were harvested without cleaning out large wood from the stream system, negative impacts to fish were mitigated and there were, in many cases, increases in fish density and biomass. This is counter to early forest management studies, which found that forest harvesting with stream cleaning, and removal of large wood, led to negative impacts and clear declines in stream salmonids (Hall & Lantz, 1969).

Given that the increases in cutthroat trout and all salmonids in our study were small when normalized to the NFHC surveys, our results do not strongly suggest that the forest management activities were a substantial benefit to cutthroat trout or *O. mykiss* populations in this system. However, consistent with conclusions about other contemporary forest management (Bateman et al., 2016, 2018; De Groot et al., 2007), our results do suggest that second-rotation forest management with riparian buffers does not lead to declines in fish relative to nearby reference watersheds. The use of NFHC as a reference in our study was appropriate given its close proximity to SFHC. However, it should be noted that this system was itself recovering from earlier forest management. Therefore, while it likely provided an accurate assessment of the overall annual trends that SFHC would have undergone through the study period, as a stream with generally young riparian forests with dense canopies, it did not necessarily reflect conditions or densities that may have been the historic norm (e.g., in late successional forests) for this system (Kaylor & Warren, 2017, 2018; Warren et al., 2016).

Cutthroat trout and *O. mykiss* responses to wildfire

In our study, we observed greater mean biomass density and mean abundance density of both cutthroat trout and all salmonids in pool habitats along the mainstem of SFHC following severe wildfire (and associated salvage logging) relative to pre-fire surveys (encompassing pre- and post-harvest periods). We observed some of the largest mean pool sizes (2022) and smallest pool sizes (2023) across the full 13-year data set during longitudinal sampling in the two post-fire survey periods (summer 2022 and 2023). We also observed one of the lower mean August baseflow discharge estimates and one of the larger mean August baseflow discharge estimates in these 2 years, thereby capturing an increase that occurred across both high and low summer discharge conditions. Independent of whether pools were larger or smaller during the post-fire period, mean fish biomass were 1.5–3 times greater in the post-fire period compared to the pre-fire periods. Comparatively, cutthroat trout and salmonid mean densities were only slightly higher in the post-fire period, which indicated that the increase in biomass was likely attributable to larger individuals rather than substantial increases in population size. The smaller number of pools identified in the two post-fire years does raise the potential for the biomass and abundance density responses observed post-fire to be an artifact of fish aggregation into a smaller number of pools. We suggest that this is not a dominant driver of our observed results given the magnitude of the post-fire responses, and because an analysis of cumulative total biomass (not normalized to pool area) yields a similar result (Appendix S1: Figure S11). In that analysis, 2022 still has strikingly high cumulative biomass even though only about three-fourths of the fish-bearing section of the mainstem was surveyed, and total biomass in 2023 was exceeded only by 2022 and 2011. Further, our observations of greater fish biomass after fire are consistent with previous research finding increased salmonid biomass, density (Gresswell, 1999; Heck, 2007; Rosenberger et al., 2015; Swartz et al., 2025).

Because the NFHC catchment also burned severely in the Archie Creek Fire, we lacked an unburned reference site that would allow us to make inferences about wildfire-impacted longitudinal profiles of biomass and abundance densities of cutthroat trout and all salmonids. Therefore, we developed a bootstrapping analysis to account for and to quantify the range of variation in the pre-fire years. We made assumptions that the range of variation over the 11 pre-fire years was likely to encompass the variation that would have occurred in the time period after the original HCPWS (2012–2021) when monitoring was discontinued. Thus, we used this analysis to develop assumptions for the potential range of fish responses that would have been expected in our study system without the occurrence of fire. When comparing the outputs from this analysis to our empirical data from the post-fire period, the observed cumulative totals for biomass density after fire were greater than almost all of the bootstrap iterations. Comparatively, cumulative totals for abundance densities after the fire were within the range of variation from the bootstrap iterations. This

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suggested that individual fish were larger after the wildfire, as opposed to biomass densities being driven by more fish. This is consistent with results from some of the sites evaluated by Swartz and Warren (2022), who also assessed effects of a severe wildfire in Oregon from 2020 in which they found that trout biomass responses were stronger than density. In that study, however, the responses were more variable across streams with observations of increases, decreases, and little change in biomass relative to pre-fire periods. In contrast to the systematic watershed-scale observations in our study, the research by Swartz and Warren (2022) focused on reach-scale responses.

Our cumulative longitudinal distribution profiles also indicate that biomass and density accumulated at a faster rate in the upper portions of the watershed in the post-fire years. Focusing on cumulative functions within individual stream segments, we found that cumulative biomass density and abundance density values in the upper reaches of the mainstem were consistently higher in the post-fire years compared to the bootstrapped iterations (specifically in segment 3 in 2022 and segment 4 in 2023). This finding suggests that the wildfire had a more substantial impact on fish populations in the upper reaches of the watershed. The greater responsiveness of the middle and upper portions of the stream may be due to greater responsiveness of fish to changing light and temperature or it may be due to smaller pool areas in the upper portions of the watershed, resulting in higher per square meter values and faster accumulation of biomass and density therefore creating a physical environment which illustrates patterns that may be occurring throughout the catchment. Interestingly, after normalizing longitudinal biomass density and abundance density patterns to the total cumulative number, creating a relative cumulative distribution between 0 and 1 for all years, we did not find any differences in distribution curves that could be explained by the major disturbances in this study.

A key driver of ecological response to wildfire is increased solar radiation and warmer stream temperatures (Bixby et al., 2015; Isaza et al., 2022; Klose et al., 2015), and in this study we saw results consistent with these findings. Summer maximum stream temperatures in the first year post-fire exceeded those seen in all three of the pre-fire periods in the mainstem (Warren et al., 2022). In the more comprehensive longitudinal assessment here, we saw daily maximum temperatures regularly exceeding 25°C lower in the basin with the magnitude of the temperature effects diminishing upstream. Yet, within the smaller headwater reaches of the system over 3500 m from the downstream confluence of SFHC and NFHC, we still saw daily maximum temperatures that regularly exceeded 20°C. This longitudinal pattern in daily maximum stream temperature is correlated with where we observed our strongest fish responses for biomass and density in pools. Elevated water temperatures can be stressful for coldwater fish and can lead to negative responses, which generally manifest as reductions in growth or abundance with rare documentation of complete extirpations associated with temperature impacts of fire (Burton, 2005; Isaak et al., 2010; Koontz et al., 2018; Swartz & Warren, 2022). However, elevated stream temperatures which do not exceed thermal tolerances of salmonids have shown to increase aerobic scope and growth in salmonids if there is enough food available (Macnaughton et al., 2021; Railsback, 2022). For example, Swartz and Warren (2022) found significant declines in adult cutthroat trout biomass in one stream following wildfire, but in another stream that saw more moderate temperature increases, cutthroat trout biomass increased substantially. The increases Swartz and Warren (2022) observed were attributed to increased solar radiation that also increased primary productivity, leading to bottom-up drivers in fish production (Mihuc & Minshall, 2005; Roon, Bellmore, et al., 2025; Swartz & Warren, 2022). Anlauf-Dunn et al. (2022) also found that cutthroat trout in Cascades streams exhibit an increase in absolute aerobic scope (defined as the absolute energy available to thrive in the environment; maximum metabolic rate—standard metabolic rate) with increases in temperature and that cutthroat trout across Oregon may be at low risk to acute thermal stress from increased stream temperatures up to 3°C above current maximum temperatures. Roon, Dunham, et al.'s (2025) bioenergetics analysis in coastal California also found evidence of cutthroat trout resilience to small increases in temperature via higher consumption rates. Although temperatures were clearly elevated in SFHC after wildfire and occasionally exceeded stressful levels, when considering the whole system over the full summer period and over the course of a given day, temperatures rarely exceeded critical thermal maxima, especially in the upper reaches (Anlauf-Dunn et al., 2022).

A major contributor to decreases in fish abundance and local extirpation after wildfire is post-fire flooding and associated debris flows (Bixby et al., 2015; Gresswell, 1999; Isaza et al., 2022); however, we saw little evidence that it was a major factor influencing fish populations in our study. Post-fire flooding has been more widely observed in other regions of North America (e,g., Rocky Mountains, SW, and California) associated with steep mountain drainages, snow-dominated precipitation, and summer and fall monsoons. In contrast, precipitation in the PNW is dominated by winter rain and in regions draining high-elevation mountains, some snow. While some storms can produce high flows, high-intensity,

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short-term rain events that would recruit high volumes of sediment from surface runoff and reorganize channels are not as common in this part of North America (Wondzell & King, 2003). Further, debris flows caused by oversaturation of soils in watersheds of Cascades typically occur 5–10 years after fire after tree roots have decayed (Wondzell & King, 2003). In Hinkle Creek, the year(s) after the 2020 fire had few large flood events relative to the historic norm in this region (Swartz & Warren, 2022), and so recruitment of sediment and ash to the streams in the first years were likely limited and thus did not appear to be a major driver when considering the short-term positive responses in cutthroat trout and salmonid biomass in SFHC after wildfire (Gresswell, 1999; Isaza et al., 2022).

The design of the initial HCPWS quantified salmonid abundances longitudinally throughout the stream network using a riverscape approach to prioritize collecting data continuously at high spatial resolution and over time (Fausch et al., 2002; Torgersen et al., 2022). This created a rare opportunity to explore fish responses broadly with sampling across the full population of salmonids along the mainstem stream. Given that wildfire impacts at the landscape scale are often patchy, creating a mosaic of disturbance severity conditions (Agee, 1996; Keane et al., 2008), research along a single stream section or stream reach may not capture the full range of potential conditions and effects. Additionally, because streams are inherently connected to riparian forests (Baxter et al., 2005), impacts of wildfire or forest management can propagate through stream networks and alter water quantity, water quality, and habitat conditions for downstream ecosystems and communities (Ball et al., 2021; Saxe et al., 2018; Wine et al., 2018). Thus, exploring stream responses to forest disturbance benefits from a spatially extensive riverscape approach (Allan, 2004; Bixby et al., 2015; Fausch et al., 2002; Torgersen et al., 2022). However, in spite of broad spatial coverage, there are limitations in the use of single-pass sampling in pools each year, which may introduce issues with spatially autocorrelated data and limit comparisons among years. Additionally, some data used for drawing pre- and post-fire comparisons have imbalanced sample sizes. Further, this study is from a single system, and while the data set is extensive, it is fundamentally a case study. Nonetheless, we suggest that results from this work have relevance in other forested systems and that by continuously quantifying longitudinal patterns in fish responses to wildfire, we provide here a more comprehensive representation of landscape effects on aquatic habitat conditions in this system and therefore a spatially relevant illustration of how fish populations respond to high-severity, large-scale disturbances (Fausch et al., 2002; Ganio et al., 2005; Schlosser, 1991; Torgersen et al., 2022).

Management implications and conclusions

In our study, we observed strong initial (within 3 years post-fire) evidence of ecological resilience in cutthroat trout and *O. mykiss* populations to both wildfire with salvage and forest management. Our results suggested that resident trout populations in our headwater ecosystem were not vulnerable to or adversely affected by these disturbances in the short term (1–3 years). Instead, we found slight (consistent, but nonsignificant) increases in overall cutthroat trout and salmonid biomass following forest harvesting activities, but much larger (significant) increases following wildfire. We attributed these increases to likely greater autochthonous basal resources and the drivers thereof, which can increase following wildfire due to increased nutrient availability (McCredie et al., 2025), and increased light fluxes due to the loss of canopy cover (Kiffney & Roni, 2007; Roon, Bellmore, et al., 2025; Swartz & Warren, 2022; Vandermyde & Whiles, 2015; Wilzbach et al., 2005). However, further research is needed to fully evaluate the extent to which these hypothesized mechanisms actually drove measured fish responses and how long these responses may persist.

Cutthroat trout and other salmonids have influenced forest management policy in the PNW for many years, particularly those policies concerning streamside harvesting and riparian buffers (Penaluna et al., 2023; Reeves et al., 2004, 2006). Although we observed an increase in cutthroat trout and total salmonid biomass following substantial reductions in overstory canopy following wildfire, canopy cover is only one aspect of forest–stream interactions (Benjamin et al., 2022). Our results suggest that cutthroat trout and *O. mykiss* in cool headwaters can be resilient to some variation in the degree of canopy cover from buffer along a stream, but it is important to note that the presence of riparian buffers remains important for several reasons. In this managed landscape, even though there was tree mortality, the high density of fire-killed snags provided a degree of shade. In addition, dead trees left in the riparian buffer provide important opportunities for large wood recruitment (Coble et al., 2024), which contributes to habitat complexity and can reduce the downstream transport of sediment. After wildfires, unmanaged riparian areas may also provide a zone with larger and more stable root structures, which may help retain mechanical cohesion of streambank soils in the short term, limiting erosion and sediment recruitment to the stream (Rieman & Clayton, 1997; Wondzell & King, 2003). Although direct effects from the interaction of wildfire with forest management were not obvious in our

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short-term study, we speculate that in this study system, the legacy of the buffer from the earlier harvests, which kept larger trees along the stream during standard timber harvests and salvage activities, likely mitigated potential negative impacts associated with sediment inputs after the wildfire and allowed for wood recruitment that created habitat and localized patches of shade over the stream where wood jams formed. Considering long-term trajectories, some key legacies of forest management may yet manifest for this system over longer time periods.

Overall, the results from our study provided unique insights into the effects of wildfire on a lotic system in a managed forest landscape of the western Cascade Mountains in Oregon, USA. This work has clear relevance to other managed and fire-prone ecosystems and will become increasingly relevant as climate conditions continue to change, but, the unique characteristics of our study site, including its disturbance and land use histories, should be considered as essential context when interpreting the results. We also stress that this study occurred in a system that did not experience a high-intensity precipitation event or large flooding event in the initial 3 years after the fire, which likely influenced these initial responses. Thus, while salmonids appeared to be resilient to wildfire disturbance in our system, it remains uncertain whether that will persist with long-term ecosystem changes following wildfire as the system recovers. Moreover, it remains uncertain whether salmonids would remain resilient if the system were to experience future disturbances in the form of reburns, debris flows, or large flooding events in future years. The potential for successive disturbances to impact the system highlights the need for continued monitoring and research, and a holistic, watershed-scale riverscape approach, which includes stream and landscape biotic and abiotic data, to fully understand the long-term impacts and adaptive capacity of trout populations to successive disturbances.

AUTHOR CONTRIBUTIONS

Jansen C. Ivie led fieldwork, led data analysis, and wrote the first draft; David A. Roon contributed to fieldwork, contributed to data analysis, and edited the manuscript; Kevin D. Bladon led grant support for post-fire research and project development, contributed to fieldwork, and edited the manuscript; David Hockman-Wert contributed to project management, data collection, data management, and analysis in the initial HCPWS from 2001 to 2011 and edited the manuscript; Dana R. Warren contributed to grant support for post-fire research and project development, contributed to fieldwork, and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ivie et al., 2026) are available from Scholars Archive@OSU: https://ir.library.oregonstate.edu/concern/datasets/gf06gb97s.

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